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Male Swarms Discovered in Chalcidoidea (Hymenoptera: Encyrtidae, Pteromalidae)

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Abstract.—Male swarms have been discovered in three chalcidoid species: *Bothriothorax nigripes, Copidosoma* sp. (Encyrtidae), and *Pachyneuron* sp. (Pteromalidae). The swarms occurred around boulders at the top of a small ridge in southern California. *B. nigripes* males, and possibly the others, swarmed for the purpose of mating. The mating behavior of *B. nigripes* is described. This may be the first report of male mating swarms in the Chalcidoidea.

Males of three chalcidoid species were discovered swarming on and around five hilltop boulders near the University of California at Riverside campus. The aggregations were discovered on March 7, 1984 and were observed at least biweekly until their disappearance in mid-April of the same year. Examination of samples taken by aspiration and aerial sweepnetting from the same location on three different days revealed the following species and numbers (males:females): *Bothriothorax nigripes* Howard (Encyrtidae), 865:23; *Copidosoma* sp. (Encyrtidae), 291:14; *Pachyneuron* sp. (Pteromalidae), 522:0. The swarms daily contained several thousand individuals of each species. They formed anew each day after disappearing entirely from the sites during the night.

This report includes a brief description of the swarming and mating behavior of *B. nigripes, Copidosoma* sp., and of the swarming behavior of *Pachyneuron* sp. Greater emphasis is given to *B. nigripes*. A study was made to determine whether the *B. nigripes* aggregations were true mating swarms. The known literature on swarming in the parasitic Hymenoptera is included in the discussion.

Swarming and Mating Behavior

I chose to closely observe *B. nigripes* to ensure that its aggregations were true mating swarms. This species is the largest of the three and thus more easily observed in the field. Males began arriving near the boulders at around 7:00 A.M. and landed during intervals of low wind velocity. Throughout the day, many swarmed in flight while others congregated on the shaded north- and northwest-facing rock surfaces. The males' behavior on the rocks consisted of walking in irregular paths with frequent turns, and beating the substrate with the antennae in rapid, alternating strokes. Landing females remained relatively motionless with their antennae tucked close to their faces, or walked slowly for a short distance (< 10 cm) before becoming still. Males encountered them within a minute or two and began courting. A schematic summary of courtship and mating behaviors is presented in Fig. 1. Males appeared to sense a female's presence from a distance of 1 cm away, as they increased walking speed and headed directly toward her from that point. Uninterrupted courtship and copulation lasted about 40 seconds. In some instances other males

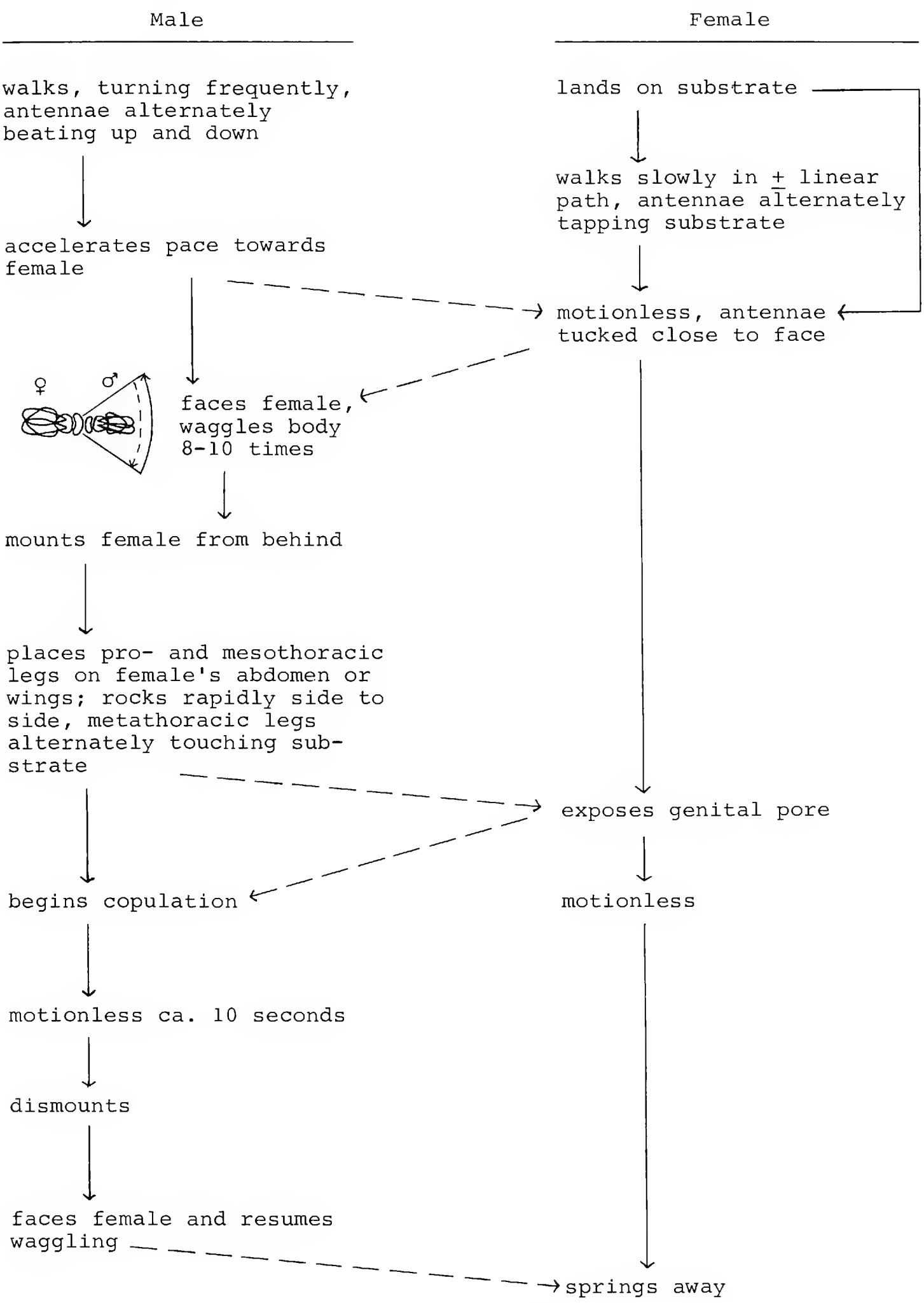

Figure 1. Schematic representation of uninterrupted courtship and mating in *Bothriothorax nigripes*.

approached a pair in apparent attempts to copulate with the female, in which case the female usually sprang away, often carrying one mounted male with her.

Females were never observed to spring away before mating or being mobbed by several males. They seemed, therefore, to arrive at the swarms specifically for the purpose of mating. To gain further evidence for this, I caught and dissected six newly-landed females (before male contact) and found that their spermathecae did not contain sperm. I paired four other newly-landed females with males in glass vials and found them to mate readily. Two of these females were dissected and found to have full spermathecae, and the remainder were paired with other males and found to reject a second mating during 9- and 18-hour video-recorded observation periods. Four additional females which were caught after they had mated naturally in the swarms also rejected subsequent mating attempts when paired with males in glass vials. Because newly-landed females mated readily both in the swarms and in the laboratory, while mated females rejected subsequent matings, *B. nigripes* females apparently join the male swarms in an uninseminated condition for the purpose of mating.

It was unlikely that females arrived in search of food; some swarm boulders were devoid of vegetation, and no feeding by either sex was observed on the few flowering plants that grew on and around the rest. It was also unlikely that females appeared in the area to search for their hosts, syrphid larvae, because none were detected on ridgetop vegetation.

I sporadically observed the other swarming species. Mating pairs of *Copidosoma* sp. were evident, often on rock-top vegetation, hence I also regarded the aggregations of this species as mating swarms. The males generally flew above or walked on the upper surface of vegetated boulders. *Pachyneuron* females, however, were neither seen nor collected. The males flew and walked around on the upper boulder surfaces, sometimes mixing with *Copidosoma,* but they also swarmed apart on the north- and northeast-facing surfaces. Although I did not observe mating within the *Pachyneuron* swarms, I suggest that, on the basis of the similarity in their aggregative behavior to the other species, the *Pachyneuron* assemblages were also mating swarms.

The Swarm Site

The most obvious factor distinguishing the swarm site, Coyote Ridge, is its situation as the only low yet abrupt peak within a 7.5 km radius. It rises 134 m above a base altitude of 335 m, and is surrounded by flat or gently sloping land. The Box Springs Mountains nearby peak at 920 m at 2.5 km to the east. A brief examination of Box Springs peaks at various heights, and of the nearest low, abrupt, hill in the area, Mount Rubidoux (165 m), revealed no chalcidoid swarms on March 24, 1984, although swarms were active that day on Coyote Ridge. Continuous and sometimes gusty winds may have contributed to the paucity of insects on the unpreferred peaks. Winds around Coyote Ridge were low and occasionally still, and perhaps more suited to controlled locomotion by the wasps.

Discussion

Male mating swarms commonly occur in insects, especially in Diptera. They are generally believed to result from 1) males searching at sites with high probability of

encounter with receptive females, such as emergence, feeding, and oviposition sites, 2) active male aggregation for the purpose of enhancing attractivity toward females, or 3) localization of mating activity at landmarks (Thornhill and Alcock 1983). Among the parasitic Hymenoptera, male swarms have been reported in the Ichneumonoidea (Ichneumonidae: Rotheray 1981; Braconidae: Donisthorpe 1936, Stelfox 1944, Southwood 1957; Aphidiidae: Stary 1970) and possibly in the Bethyloidea (Dryinidae: Jervis 1979), but not in the Chalcidoidea. Large swarms of female *Cyclogastrella* (= *Pteromalus*) *deplanata* (Pteromalidae) have been reported from buildings in England (Scott 1919), and of female *Chrysocharis centralis* (Eulophidae) on vegetation in Madeira (Graham 1983), but there is no indication that these served a mating purpose. Recently, however, pteromalid mating swarms have been observed on citrus trees in China (J. K. Waage, personal communication).

The male chalcidoids on Coyote Ridge appeared to use either a landmark-based swarm site and/or to aggregate to increase their power to attract females. There was no indication that either sex arrived at the ridgetop to feed. Similarly, at least for *B. nigripes,* there was no indication that females arrived in search of hosts. Certainly, there was no indication that the ridgetop was in any way more profitable than the surrounding areas in terms of food or oviposition sites for any of the swarming chalcidoids. The ridgetop, however, offers a distinctive landmark which is also accompanied by slower winds than those which prevail on the nearest peaks. It is, therefore, not only conspicuous, but also allows controlled locomotion by the insects. These attributes of the ridge may have set the stage for the evolution or maintenance of a landmark-based mating system in the observed chalcidoids. It is also possible, however, that the males of each species aggregate because they thus have a greater chance of mating than if they remained solitary. Male aggregation pheromones are commonly implicated in the formation of insect swarms and in the attraction of females (Thornhill and Alcock 1983). It is not impossible that the aggregation pheromones, if they exist, of the three studied chalcidoid species are similar; this would explain why these presumably rare swarms occurred together. Much more work is necessary to reveal why and how the swarms occur, but at this point the observations indicate that they are part of a landmark-based mating system or the result of a male tendency to aggregate, or both.

Chalcidoid mating swarms have been reported here for the first time, but is this because little attention has been given to parasitoid mating behavior in nature, or is it because the swarms are truly rare? As far as I know, there have been no focused studies on the mating systems of non-inbreeding parasitic Hymenoptera beyond the confines of the laboratory. This is unfortunate from both a practical and theoretical standpoint. Such studies may aid the evaluation of biological control agents; introduced exotic chalcidoids, for example, may fail to become established because of the absence of proper mating sites. As I showed in this study, readiness to mate in the laboratory gives no indication of the species' mating system: *B. nigripes* mated readily in glass vials. If chalcidoid mating swarms are truly rare, however, we should search for a general tendency in the Chalcidoidea to mate at the emergence site rather than to mate after dispersal. Many chalcidoid species have a preponderance of females (Gordh 1979), and this has been linked, in theory, to pre-dispersal mating (Hamilton 1967, Charnov 1982, Waage 1982). The discovery of chalcidoids which mate away from their natal site paves the way for testing the relationship between

mating system and sex ratio in this group. In any event, the study of chalcidoid mating systems should provide a rich store of information for both practical and theoretical work.

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